

Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours

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Habitat selection and dispersal behaviour are key processes in evolutionary ecology. Recent studies have suggested that individuals may use the reproductive performance of conspecifics as a source of public information on breeding patch quality for dispersal decisions, but experimental evidence is still limited for species breeding in aggregates, i.e. colonial species. We addressed this issue by manipulating the local breeding success of marked individuals and that of their neighbours on a series of breeding patches of a colonial seabird, the black-legged kittiwake (*Rissa tridactyla*). Based on previous observations in this species, we predicted that individuals that lost their eggs on successful patches would attend their nest and come back to it the year after at a higher rate than individuals that lost their eggs on patches where their neighbours were also in failure. As predicted, the attendance of breeders and prospectors was strongly affected by the local level of breeding success, resulting in differential site fidelity and recruitment. This suggests that individuals used information conveyed by conspecific breeding performance to make decisions relative to breeding site selection. This process can amplify the response of these populations to environmental change and may have contributed to the evolution of colonial breeding.

Keywords: breeding habitat selection; coloniality; prospecting; conspecific performance

1. INTRODUCTION

Habitat selection and dispersal are key processes for understanding population responses to environment variability (Clobert *et al.* 2001; Kokko & Lopez-Sepulcre 2006). The selection of a suitable breeding habitat is indeed essential for the reproductive success of most animals, notably territorial birds (Jones 2001). Proposed cues for territory selection by birds include habitat

characteristics and individual experience, such as birth place or previous individual breeding performance (Greenwood & Harvey 1982; Switzer 1993). Social cues may also influence habitat selection (Hahn & Silverman 2006; Seppänen *et al.* 2007). In particular, it has been suggested that individuals can use the reproductive success of conspecifics as a source of public information on breeding patch quality (Danchin *et al.* 1998; Doligez *et al.* 2002). Despite several observational studies (e.g. Danchin *et al.* 1998; Schjørring *et al.* 1999; Brown *et al.* 2000; Serrano *et al.* 2004), experimental evidence is nevertheless still limited for species breeding in colonies (Aparicio *et al.* 2007). Colonial species breed in aggregates of breeding-only territories and feed on non-defensible food outside the colony. In such species, the local performance of conspecifics may thus be a particularly reliable source of information about the quality of potential breeding patches (Boulinier & Danchin 1997).

Populations of seabirds are naturally subdivided at different spatial scales and represent good models to study these processes. Detailed observations on a kittiwake *Rissa tridactyla* population in Brittany, France suggested that individuals use the reproductive success of their conspecifics, or some social correlates, for selecting among potential breeding patches (Danchin *et al.* 1998). Failed breeders and young prospecting birds were suspected to be attracted to successful areas to breed and disperse from unsuccessful patches, but the observational data used in this study did not enable the identification of the causal nature of the observed associations. The behaviour of the birds could have been affected directly by the natural causes behind the differences in the breeding success (e.g. local predator activities) and not by the differences in the breeding success itself (Doligez *et al.* 2002). In the present work, we addressed this issue experimentally. Specifically, we manipulated the local reproductive success of kittiwakes on a set of study plots in order to test the behavioural responses of the birds in terms of (i) attendance of local breeders and prospecting individuals the year of the manipulation and (ii) dispersal versus site fidelity the year after.

2. MATERIAL AND METHODS

The study was conducted on Hornøya (70°22' N, 31°10' E), an island in the northeast of Norway, where more than 10 000 pairs of kittiwakes breed (Boulinier *et al.* 2002). Kittiwakes are pelagic seabirds that come back annually to breed on sea cliffs on which they build their nest. They lay a clutch of one to three eggs. Individuals start breeding at an age of 3 or 4 years and show high overall breeding site fidelity (Danchin *et al.* 1998). Individuals can be captured to be colour ringed when they brood eggs or young chicks (figure 1a). Colonies are often subdivided into sub-colonies of tens of nests, among which individuals can socially interact.

The principle of the experiment was to follow the fate of marked breeding individuals put in failure on sub-colony patches where the local breeding performance was experimentally manipulated. Breeding birds were thus captured and marked during the breeding season of 1998 on a series of nine pairs of breeding plots (figure S1 in the electronic supplementary material). The year after, treatments were randomly attributed to individual nests and plots (i.e. following a block design). Plots were paired both spatially and by size (mean plot size: 42.3 ± 25.8 breeding pairs). Within each pair of study plots, one plot was randomly chosen to be put in failure and the other was left or maintained in success. Manipulations of nest contents were performed at the egg stage, for which we expected the strongest behavioural response of failed breeders (Danchin *et al.* 1998). Within plots to be put in failure, eggs were removed from all nests. Within plots to be left in success, only nests of focal birds (i.e. those with colour-marked breeders) were put in failure.

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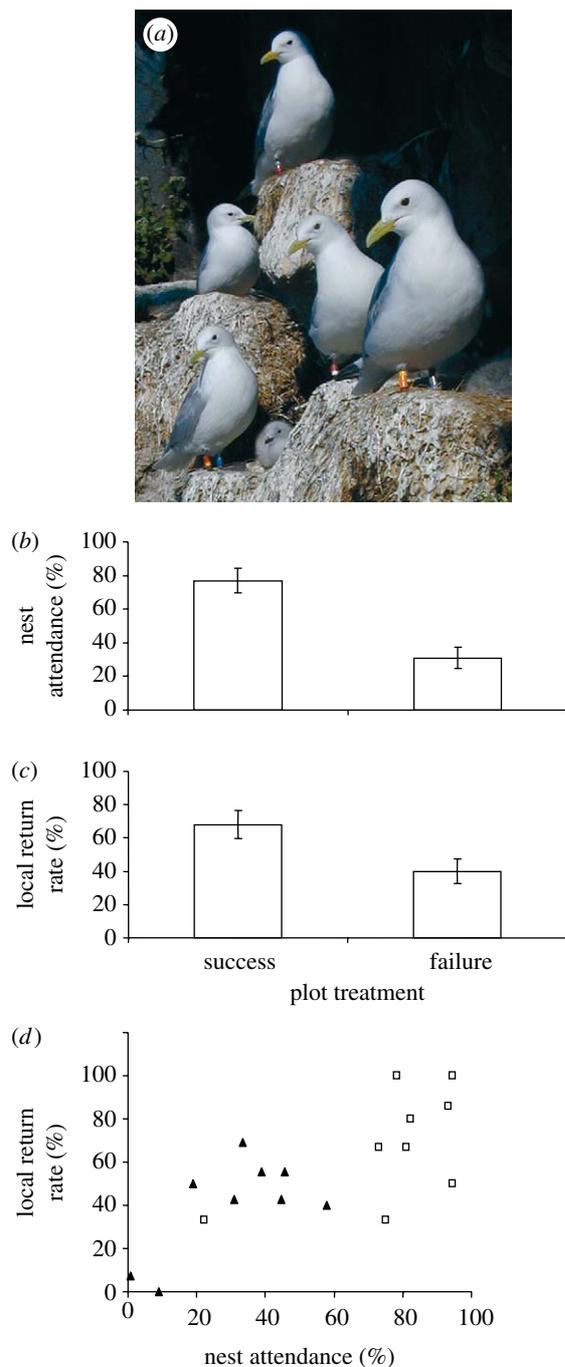


Figure 1. (a) Colour-ringed kittiwakes attending their nests (photograph copyright T. Boulinier). (b) Nest attendance during chick rearing (\pm s.e.) on patches where the local performance of conspecifics was experimentally maintained high compared with patches where it was set low. (c) Local return rate of failed breeders 1 year after the experiment (\pm s.e.) on patches where the local performance of conspecifics was maintained high compared with patches where it was set low. (d) Relationship between breeder attendance on failed nests at the end of the season and local return rates of breeders the year after on patches where the local performance of conspecifics was experimentally set low (triangles, plots in failure) or maintained high (squares, plots in success).

In failed nests, eggs were removed after the first egg laid had been brooded for 25 days and then every sixth day. In some instances, to compensate for natural failures in successful plots, eggs were moved to nests that had been emptied by predators in the last 24 hours. This manipulation led to contrasted local levels of reproductive failures within all plot pairs, but one, where predation by ravens *Corvus corax* prevented us from maintaining a reasonable

reproductive success in the 'successful' plot. The proportion of successful nests thus varied between 0.26 and 0.74 for the nine plots 'in success' (mean \pm s.e. = 0.55 ± 0.05) and was null on the nine corresponding unsuccessful plots (all eggs were removed, including those of replacement broods). Care was taken to expose birds within each pair of plots to comparable levels of disturbance.

Breeder attendance to their nest was recorded during the year of the treatment (1999) and return rate to their breeding plot was assessed during the next season (2000). By comparing the local attendance and return rate of failed breeders from pairs of plots where their neighbours had been put in failure or left in success, we thus mimicked a natural situation often observed in the study species (Danchin et al. 1998; Suryan & Irons 2001) to investigate factors affecting dispersal without having to track the dispersing individuals themselves. The interpretation of data regarding the prediction about differential site fidelity between plot treatments relies on the reasonable assumption that the local survival rate of the marked birds did not differ within pairs of plots. The monitoring of marked individuals on the plots every third day and the use of closed population models enabled us to check that all local breeders were detected (Boulinier et al. 2002).

Mixed models were used to model both the daily nest attendance (present or not on the nest) and the local return rate (returned or not to breed on the same patch the year after) of focal breeders. We included plot pair and treatment, respectively, as a random and a fixed factor in the analyses. Breeding site and date (Julian day) were also included, respectively, as a random and a fixed factor in the attendance model. We checked that there was no difference in attendance between plots within plot pairs at the beginning of the season (i.e. before the egg removal treatment was applied). Further, no effect of the mean egg size of individuals was detected on the behavioural responses studied, indicating that responses did not vary strongly with this measure of individual 'quality'.

3. RESULTS

As predicted, we found a lower attendance of local breeders following their breeding failure in plots assigned to failure compared with plots where success was maintained (figure 1b; effect of neighbour performance on nest attendance after 29 June: $F_{1,8} = 56.5$, $p < 0.001$). Several failed breeders from unsuccessful plots were recorded prospecting for sites outside their plot and settled on new plots the year after.

We also found that failed breeders on successful plots returned to breed locally the year after at a higher rate than failed breeders on unsuccessful plots (figure 1c; effect of neighbour performance on return rates $F_{1,8} = 7.06$, $p = 0.03$). Overall, 28 failed breeders out of a total of 40 (72.5%) came back to their successful plot the year after, when compared with 51 failed breeders out of a total of 106 (46.8%) on unsuccessful plots.

Finally, there was a positive relationship between the level of nest attendance at the end of the breeding season and the probability of local breeders returning to build a nest on the same breeding plot (figure 1d; $r = 0.73$, $p < 0.001$).

4. DISCUSSION

We found compelling evidence of the use of public information for breeding habitat selection in a colonial species. By manipulating the local breeding success on a series of sub-colony plots, we experimentally addressed whether individuals that failed in their reproduction used the reproductive success of conspecifics as a source of public information on breeding patch quality for decisions relative to site fidelity. We found that attendance of individuals at breeding sites at the end of the season of the year of the manipulation, and subsequent plot fidelity the year after, were affected by the local performance of conspecifics.

The return rates of local failed breeders that we recorded were high, but comparable to rates reported in natural circumstances (e.g. Danchin *et al.* 1998). The proportion of failed breeders that came back to start breeding on the same plot the year after was correlated with the local nest attendance on failed nests at the end of the season the year before, at a time when failed individuals can be recorded prospecting on patches to which they may eventually disperse (Boulinier *et al.* 1996; Danchin *et al.* 1998). The experimental approach was thus successful at showing the suspected causal nature of the behavioural patterns reported previously. Studies at larger spatial scales would now be important.

The occurrence of such habitat selection processes shows that individual behaviour is a key element to consider for understanding the dynamics of subdivided populations, with implications ranging from the evolution of colonial breeding to the conservation of fragmented populations. In species feeding on non-defensible resources, such as seabirds, the advantage of settling close to successful conspecifics in environments where high-quality patches are scarce, but patch quality is temporally autocorrelated, may have contributed to the evolution of coloniality (Boulinier & Danchin 1997). Habitat selection based on conspecific performance will directly affect the temporal distribution of individuals among potentially suitable patches, and thus population persistence (Schmidt 2004). The use of conspecific performance as a cue to assess habitat quality may indeed prevent individuals from falling into an ecological trap as this information should enable them to reliably track environment change (Kokko & Sutherland 2001). Alternatively, it could also increase the extinction risk of subdivided populations by aggregating individuals on a few suitable areas. In both cases, the results presented here emphasize that understanding the behavioural processes underlying life-history decisions, and notably the use of social information by individuals (Valone & Templeton 2002; King & Cowlshaw 2007), is critical for predicting the response of populations to environment variability.

All work was carried out in accordance with standard animal care protocols and approved by the Ethical Committee of the French Polar Institute. Permits to manipulate nest contents of Kittiwakes and conduct the experiment were granted by the Norwegian Animal Research Authority.

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